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Predatory Behavior of *Gasteracantha mammosa* C. KOCH (Araneae: Araneidae)

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吉田　真[1)]：チブサトゲグモの捕食行動

Abstract : The predatory behavior of *Gasteracantha mammosa* (Araneae: Araneidae) was investigated. This species did not immobilize its prey by wrapping at all, and always immobilized them by biting. It could capture bees, though they stung it. The spider seemed not to be influenced by the stinging at all, perhaps because of the hard body. But the spider could not capture pentatomids in most cases, apparently because of the stink.

This species did not carry its prey suspended on a silk line at all, and large prey were usually pulled to the hub along a radius. This curious carrying method resembled the carrying method of *Theridiosoma epeiroides* (Theridiosomatidae).

ROBINSON, MIRICK and TURNER (1969) compared the predatory sequences of several araneid spiders such as *Nephila clavipes* and *Argiope argentata,* and showed that some species use wrapping for their prey immobilization but others do not use such type of wrapping. They called it as "immobilization wrapping" or "attack wrapping", and supposed that it has been derived from the wrapping at the capture site after attack bite. So, *Nephila* and *Micathena,* which do not use attack wrapping, are thought to be in the primitive stage of the evolution of predatory behavior. As ROBINSON (1975) pointed out, of course, it does not mean that *Nephila* or *Micrathena* is the ancestor of *Argiope* or *Araneus,* which uses attack wrapping, but it only supposes that the ancestors of *Argiope* or *Araneus,* as well as *Nephila* or *Micrathena,* did not use attack wrapping.

The lack of attack wrapping in *Nephila* and *Micrathena* can be explained by following two contradictory manners each other. First, these species remain in the primitive stage of the evolution of predatory behavior (ROBINSON, MIRICK and TURNER, 1969; ROBINSON, 1975). Next, they have lost the habit of attack wrapping secondarily, though their ances-

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tors used attack wrapping. Levi (1978, 1985) explained the lack of attack wrapping in Gasteracanthinae, including *Gasteracantha* and *Micrathena*, with the second explanation.

Whether *Gasteracantha* uses attack wrapping or not, has not been studied yet in detail. From the observation of Muma (1971), Robinson (1975) listed *G. cancriformis* as a species using attack wrapping. On the contrary, Eberhard (1982) gave 20 prey (including dangerous insects such as wasps and bees) to *G. cancriformis*, and demonstrated that it does not use attack wrapping. Levi (1985) also stated that *Gasteracantha* and *Micrathena* do not use attack wrapping.

In spring 1987, I studied the predatory behavior of *G. mammosa* for several days. By the study, it was demostrated that this species did not use attack wrapping at all. Futhermore, I found that this species did not carry large prey suspended on a silk line from the spinnerets, but carried it by a curious method of transportation. So, I report the results in this paper, and discuss how the origin of the lack of attack wrapping and the curious carrying method can be explained.

Materials and Methods

The investigation was done from late March to early April 1987 in Ryukyu Islands. Various kinds and sizes of prey were given to the webs mainly of the adult females of *G. mammosa*, and the predatory behavior of them was observed. The prey given were Orthoptera, Lepidoptera, Diptera, Coleoptera, Hemiptera (pentatomids), Hymenoptera (bees and wasps), Ephemeroptera and Trichoptera. Each prey was less than 2.5 times body length of the spider.

When natural prey were caught in the web, the predatory behavior to them was also observed. The natural prey of the species were collected from the webs. If the prey were not destroyed by the spider, they were identified and their body length was measured later in the laboratory. The prey, which were bitten and half-digested by the spiders, were identified by the part(s) of the body, if possible. Then the size was roughly estimated.

Results

1. The predatory sequences employed

Following three sequences for prey immobilization were observed;

Seize-Pull out (SP); Spider seized the prey in the jaws, and then pulled it from the web immediately.

Bite-Pull out (BP); Spider bit the prey for several to several tens seconds. Then the spider bit various parts of the prey, bent the prominent parts of the prey, and cut the tangled silk. Finally, the spider pulled the prey by the jaws from the web.

Bite-Wrap (BW); Spider bit the prey for several seconds to a minute. Then the spider bent the abdomen to wrap the prey with silk, while it was still in the jaws. Then the spider released it from the jaws and wrapped the prey. The spider usually could not pulled the prey from the web with the jaws, because the prey was tangled by both the spiral silk of the web and the silk used for wrapping. So, it cut the entangled silk from the prey, using the jaws and the first legs. Only the outside part of the web was cut out (Fig. 3A).

2. The capture efficiency and the frequency of each sequence for prey immobilization

Table 1 shows the response of *G. mammosa* to various types of prey. Of the three sequences, BW was applied more frequently than both SP and BP. The spider caught 64% of the prey on an average which were restrained by the web. But the percentage (the capture efficiency in Table 1) was various with the types of the prey; that is, there was the high efficiency group (Lepidoptera, Diptera and Orthoptera) and the low efficiency group (Coleoptera and Pentatomidae). The efficiency of Hymenoptera including honey bees was intermediate. There were two types of pentatomids. One type could be distinguished by the stink like acetic acid from another type. The capture efficiency to the former pentatomids was very high, though the sample size was small. On the contrary, that to the latter pentatomids was very low.

Table 1 The predatory behavior of *Gasteracantha mammosa*. SP : Seize-Pull out, BP : Bite-Pull out, BW : Bite-Wrap.

Prey	Spider neglected or rejected the prey. Or prey escaped.	SP	BP	BW	Total	Capture efficiency (%)
Orthoptera	3	0	1	9	13	76.9
Lepidoptera	0	0	0	7	7	100.0
Diptera	2	6	8	19	35	94.3
Coleoptera	10	0	1	1	12	16.7
Hemiptera (pentatomids)	17	0	1	4	22	22.7
Hymenoptera (bees and wasps)	4	1	1	2	8	50.0
Ephemeroptera	0	0	1	0	1	100.0
Trichoptera	0	0	0	2	2	100.0
Total	36	7	13	44	100	64.0
Pentatomids giving out :						
Stink as acetic acid	1	0	0	3	4	75.0
Other stink	16	0	1	1	18	11.1

Table 2 The predatory behavior of *G. mammosa* to pentatomids. Pentatomids were divided into two groups, based on whether they had given out the stink as acetic acid or not. The numerals in parentheses show the number of cases observed.

1) The kinds of pentatomids which gave out the stink not as acetic acid (18)
  A) The cases in which the stink was not perceived by observer (10)
    Spider neglected or rejected the prey and/or it escaped from the web (8)
      Spider did not response at all (1)
      Prey dropped after (by?) pluking of the web (1)
      Spider approached. tried to bite the prey, then returned to the hub (1)
      Spider approached and touched the prey (5)
    Bite-Pull out (1)
    Bite-Wrap (1)
  B) The cases in which the stink was perceived by observer (8)
    Spider neglected or rejected the prey and /or it escaped from the web (8)
      Spider approached, The prey gave out the stink, and then the spider returned to the hub (2)
      Spider approached, touched the prey. The prey gave out the stink, and then the spider returned to the hub (2)
      Spider approached, touched and tried to bite the prey. The prey gave out the stink, and then the spider returned to the hub (1)
      Spider approached, bit the prey. The prey gave out the stink, and then the spider returned to the hub (3)

2) The kinds of pentatomids which gave out the stink as acetic acid (4)
  A) The cases in which the stink was not perceived by observer (1)
    Spider neglected or rejected the prey and/or it escaped from the web (1)
  B) The cases in which the stink was perceived by observer (3)
    Bite-Wrap (3)

As shown in Table 2, when the stink of the latter pentatomids was perceived (by the observer), spider could not capture them at all. The stink of the pentatomids seemed to damage the spider strongly. When the stink was given out, the spiders ran away to the hub, and rubbed the face with their legs frequently. In one of the cases, the spider was suspending from the hub with the right first leg, and was probably fainted away for several minutes. Even when the stink was not perceived (10 examples), the spider could not (did not?) capture them in 8 examples. In several cases, the pentatomids might give out the stink for a little, though it was not perceived by the observer. On the contrary, though the pentatomids with the stink like acetic acid apparently was given out the stink, the spider captured them in most cases (3/4).

Fig. 1 shows the relationship between each sequence to immobilize the prey and the relative size (prey/spider) of various prey. SP was usually applied to small prey (especially to Diptera), on the other hand, BW was applied to relatively large prey. BP was applied mainly to small prey, but sometimes to fairly large prey. There was the difference in the number of the sequences as to the types of prey; that is, one type (such as Diptera and Hymenoptera) to which all sequences were applied, and another type to which only one or two sequences was applied. Of the latter type, Lepidoptera was attacked only by BW. The size of the prey captured by the spider seemed to be not very different from that of the prey not captured by the spider, except very large prey (pentatomids, Hymenoptera and Coleoptera) which were not captured at all (Fig. 2).

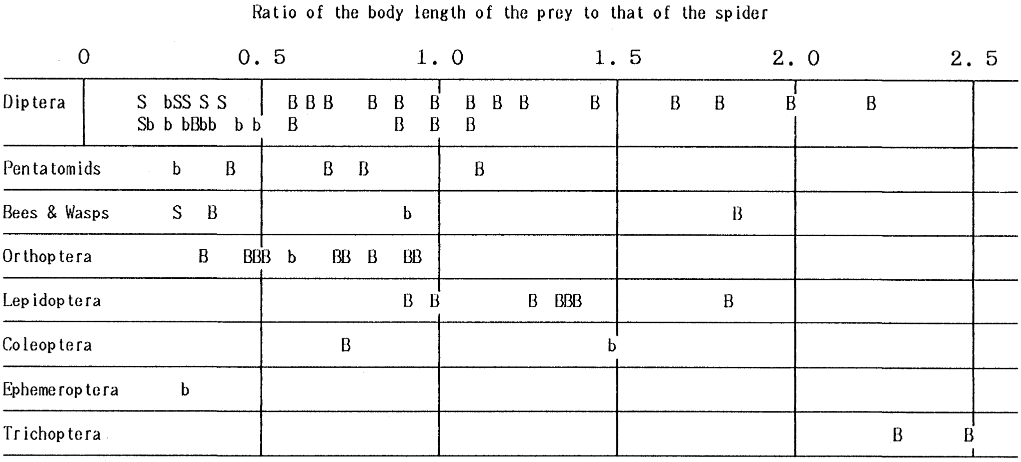

Fig. 1 The relationship between each predatory tactics to immobilize the prey and the relative body length (prey/spider) of various kind of prey. S : Seize-Pull out, b : Bite-Pull out, B : Bite-Wrap.

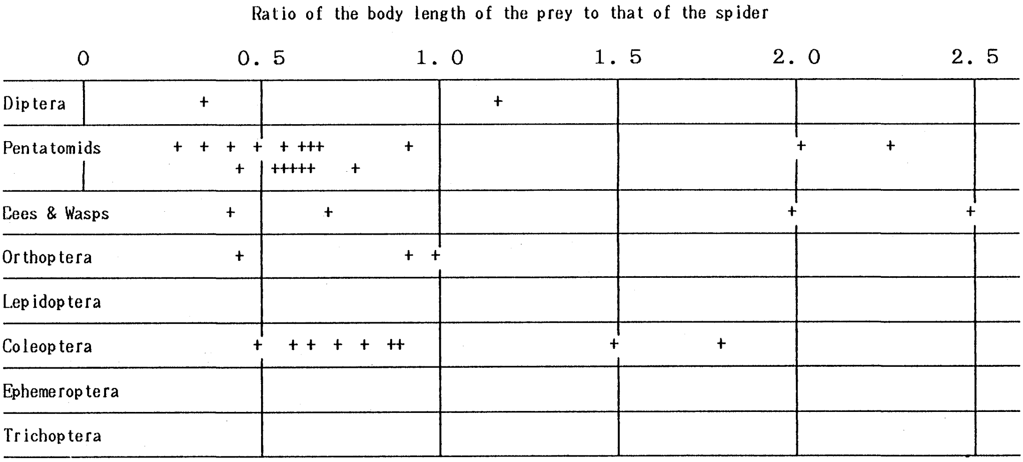

Fig. 2 The relative body length of various prey not captured by the spider.

3. The methods of transportation

This species sometimes did not carry the prey after the prey immobilization, but left them at the capture site and returned to the hub. If there was the prey at the hub, captured earlier and suspended from the hub by a silk line, the spider fed it. Most prey, left at the capture site were carried later to the hub after several tens minutes to a few hours. There were various methods of transportation as follows :

(1) The spider did not carry the prey to the hub soon after the immobilization (Leaving the prey : L).

(2) The spider carried the prey soon after the immobilization by following methods:

  a. Carrying the prey in the jaws (Cj).

  b. Pulling the prey near the hub, using the first and second legs, from the hub (Ph).

  c. Cj and Ph. The spider carried the prey in jaws, but the prey was tangled by the hub. So, the spider returned the hub, and pulled the prey from the hub with the legs I and II (CjPh).

Following methods of transportation (d-1) include some new specific behavioral units. They have been not observed in other araneids, so I describe them before the explanation of d-1.

Behavioral units :

A : Cutting off the web (spinning a silk line between the prey and the frame thread) : The outside part of the web was cut off. The radius, to which the prey was bound, is not cut (Fig. 3A). If the radius was cut during prey-immobilization, a silk line was spinned between the prey and the frame thread.

X : The spider attached a silk line to the prey, walked along the web to the hub, pulling the prey with a silk line spinned from the spinnerets. The spider then attached the silk line to the hub. Consequently, the prey was drawn a little to the hub. This behavior

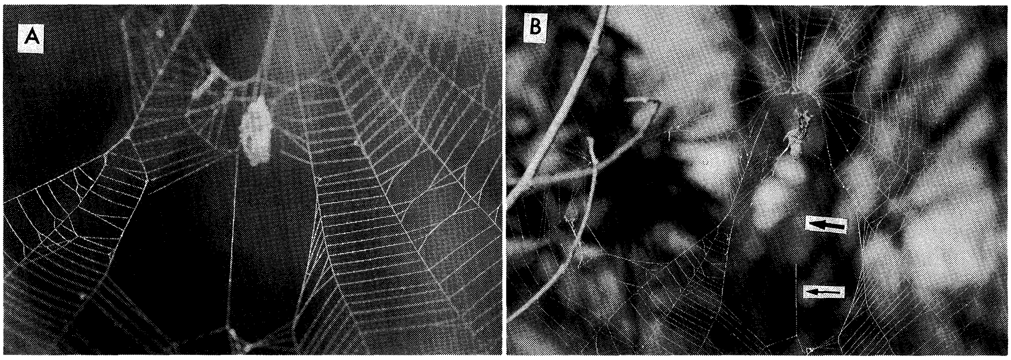

Fig. 3 Carring method for large prey. The web is sprayed with lacquer paint. A : Cutting of the outside part of the web. The radius, to which the prey was bound, is not cut. B : The addition of a silk line newly made between the prey and the radius (shown by→). The additional silk line is not visble in the photograph (shown by➔), because it is not sprayed with laquer paint.

resulted both in the partial destruction of the web on the way and in the increase in the tension of the silk line spinned by the behavior "A".

Y : This behavior occured after "X" in most cases. The spider spinned a silk line, attaching the end to the hub, and walked to the prey along the silk line spinned by "X". The spider walked, pulling the silk line "X" to the prey, so the prey was drawn to the hub a little consequently. The silk line spinned by "Y" (shorter than that spinned by "X", of course) was finally attached to the prey. This behavior also resulted in the increase in the tension of the silk line spinned by "A".

Z : The spider cut the radius outside of the prey, then added a new silk line between the radius and the prey. The prey was drawn to the hub a little, because the new silk line was added (Fig.3B).

The methods of the transportation, including the above behaviral unit (s) were divided into the several patterns as follows :

The cases in which "X" was included but "Y" and "Z" were not included :

d . XPh (Spider carried first with X, then with Ph)

e . XCjPh (Spider carried first with X, then with Cj and Ph)

The cases in which "X" and "Y" were included but "Z" was not included :

f . XY (Spider carried first with X, then with Y. This method consisted of XY and XYXXY)

g . XYCj (Spider carried first with XY, then with Cj. This method consisted of XYXYCj)

h . XYPh (Spider carried first with XY, then with Ph)

The cases in which "X", "Y" and "Z" were included :

i . XYZ (Spider carried first with XY, then with Z. This method consisted of XYZXY,XYZXYXY and XYZXYXYXY)

j . XYZCj (Spider carried first with XYZ, then which Cj)

k . XYZPh (Spider carried first with XYZ, then with Ph. This method consisted of XYZXYZPh)

The case in which only "z" was included :

l . ZCj (Spider carried first with Z, then with Cj)

Fig. 4 shows the relationship between the method of transportation and the type or size of the prey. Cj was used frequently to the relatively small prey, on the contrary, the methods including the specific behavioral units (X,Y,Z) were used mainly to the relatively large prey. This species seemed not to use the special method to the special type of prey. Table 3 shows the relationship between the prey immobilization tacticses and the carrying methodes. In the case of SP and BP, that is, if the spider pulled the prey out of the web,

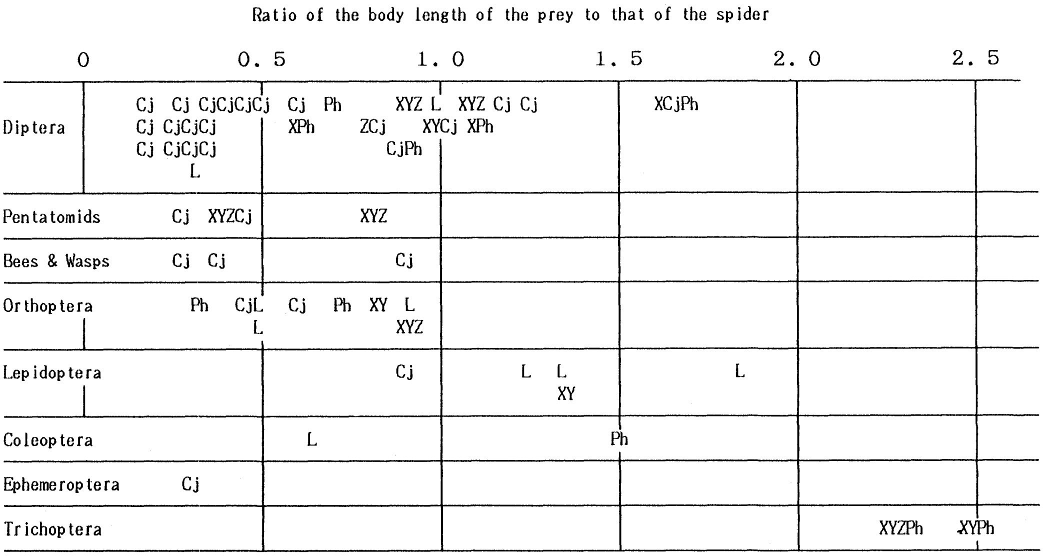

Fig. 4 The relationship between the carrying methods and the relative body length (prey/spider) of various kinds of prey. See the text for the explanation of symbols.

Table 3 The relationship between the predatory sequences and the carrying methods in *G. mammosa*. See the text for the explanation of the symbols.

Predatory sequences	SP	BP	BW
Carrying methods			
L	0	0	9
Cj	7	12	6
Ph	0	0	3
CjPh	0	0	1
XPh	0	0	2
XCjPh	0	0	1
XY	0	0	2
XYCj	0	0	1
XYPh	0	0	1
XYZ	0	0	4
XYZCj	0	0	1
XYZPh	0	0	1
ZCj	0	0	1

all the prey were carried in jaws (that is, Cj). On the other hand, if the spider used the tactics BW, it carried the prey by various methods (including prey-leaving at the capture site).

4. The kinds and the size of the prey captured in the webs in natural condition

Table 4 shows that Diptera, Hymenoptera, Coleoptera were the main prey of the spider, Lepidoptera was few, Pentatomidae and Orthoptera were absent. The majority of the prey was smaller than 7.5mm, and the prey larger than 15mm was absent. Since the adult spiders were about 10mm in body length, most of the prey were smaller than spiders.

Table 4 The natural prey collected in the webs of *G. mammosa.*

	Body length (mm)					
	0−2.5	2.5−5.0	5.0−7.5	7.5−10.0	10.0−15.0	Total
Diptera	7	10	8	0	0	25
Bees & Wasps	2	1	6	3	6	18
Winged ants	0	1	0	0	0	1
Coleoptera	5	6	2	1	0	14
Coleoptera (larva)	0	1	0	0	0	1
Aphids	4	0	0	0	0	4
Lepidoptera	0	0	0	0	2	2
Ephemeroptera	0	0	1	0	0	1
Total	18	19	17	4	8	66

Discussion

The predatory behavior of *G. mammosa* is characterized by the lack of attack wrapping, the curious carrying method and the lack of the transportation of the prey suspended on a silk line from the spinnerets. The low efficiency in capturing pentatomids is apparently due to the lack of attack wrapping and the stink of pentatomids, though *G. mammosa* can capture the pentatomids which give out the stink like acetic acid. Pentatomids were not found in the webs of *G. mammosa* at all, so they seems not to be the prey of the spider in natural condition. Beetles were found frequently in the webs, though the efficiency in capturing them (given by me) was low. It is probably due that most of the beetles found in the webs were smaller than that given by me and perhaps easy to capture. It is interesting that bees and wasps were found frequently in the webs. The spider captured the half of bees and wasps given by me. I observed that the spider captured a honey bee about two times longer than the spider in body length. The spider bit the ventral side of the bee's thorax, and the bee stung the ventral side of the spider's abdomen several times. But the spider seemed not to be influenced by the stinging at all, perhaps because of the hard body. It means that bees and wasps are not always dangerous for the spider. They, as well as Diptera and Coleoptera, seem to be a main prey for the spider.

The lack of attack wrapping can be explained by two manners ; that is, it may be a primitive character in the evolution of predatory behavior (Robinson, Mirick and Turner, 1969 ; Robinson, 1975), or it may have been secondarily lost (Levi, 1978, 1985).

But, if the latter explanation is true, why have they lost the habit of attack wrapping? Robinson (1975) listed the main two functions of attack wrapping as follows : (1) The spider can attack large and/or potentially dangerous prey without the dangers involved in the intimate contact of a biting attack. (2) The spider reduces the time spent away from the hub in predatory sequences. Surely it is difficult to imagine why the ancestor of *Gasteracantha* abandoned attack wrapping, if it had the highly developed swathes of silk, as found in *Argiope* and *Araneus*. But, if it had the poorly developed swathes of silk as found in *Leucauge,* the lack of attack wrapping might occur more easily, because the attack wrapping of *Leucauge magnifica* looks like less effective (Yoshida, unpublished data). Furthermore, the importance of the functions of attack wrapping may be dependent on the extent in the prey specialization of the spider : that is, if the spider usually does not capture dangerous prey, the first function must be less important. As stated earlier, the main prey of *G. mammosa* seems to be Diptera, Coleoptera and Hymenoptera. Bees and wasps seem not to be dangerous prey for the spider, perhaps because of the hard body. Pentatomids are dangerous for the spider because of the stink, but they seem not to be the prey of the spider. I can not decide now whether the lack of attack wrapping is primitive or derived. In order to solve the question, we must get more information about the morphological and the behavioral characters in Gasteracanthinae which includes such genera as *Gasteracantha, Micrathena, Chaetacis.*

Why doesn't *G. mammosa* carry large prey suspended on a silk line, though this carrying method is common in Araneidae? And why does it carry them with the curious method, shown in results? The latter method takes long time for the spider to carry them to the hub. And it results in the destruction of the part of the web on the way from the capture site to the hub. It looks like absurd way for me. The function of the curious carrying method is unclear. Shinkai and Shinkai (1985) observed similar carrying method used by *Theridiosoma epeiroides* (Theridiosomatidae) : "This spider fixed the prey to a radial thread, made the thread (between the frame thread and the prey) longer, drew the thread (between the prey and the hub) to the hub. So, the prey was gradually carryed to the hub." Similar method is also seen in theridiid spiders such as *Achaearanea* and *Theridion* (Shinkai, personal communication). Whitehouse (1986) called the behavior observed in *Argyrodes antipodiana* as "Hoisting". Well, *G. mammosa* is a member of Araneidae, and quite different from Theridiosomatidae or Theridiidae morphologically. So, the similariry of the carrying methods must mean that it is convergence. If it is true, it means that the ancestor of *G. mammosa* abandoned the method by which the prey was carried, being suspended on a silk line, and that the spider began to carry the prey by the curious method. Or, does it indicate that some phylogenetic relation among *Gasteracantha,* Theridiosomatidae and Theridiidae? In order to solve the question, we need at least to get more information about the carrying methods of the other species of *Gasteracanthinae*. The thorough study on various morphological and behavioral characters of the subfamily will solve the question in future.

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摘　　要

チブサトゲグモは、もっぱら噛みつき(Bite)によって網にかかった餌を固定し、固定のために糸の巻き付け(Wrapping)を全く行なわなかった。コガネグモ科の他の種は大きな餌を糸にぶら下げて運搬するが、この種はそのような方法を取らず、縦糸に添って餌をコシキに徐々に引き寄せる独特の運搬方法を示した。

この種は、おそらくは身体が堅いために、身体を刺されても平気でミツバチを捕らえた。しかしこの種は、強烈な匂いのためにカメムシの多くを取り逃がしていた。このことは、固定Wrappingの欠如がハチの捕獲に不利にならないが、カメムシの捕獲には不利になることを示している。

この種の奇妙な運搬方法の機能は不明であり、今後近縁の属のそれを調査しそれと比較すべきであろう。

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